

## THE SPATIAL DYNAMICS OF LINYPHIID SPIDERS IN WINTER WHEAT

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The density of linyphiid spiders was monitored accurately throughout the growing season in a field of winter wheat in southeast England in 1990 and 1991. Numbers increased until harvest in 1991, but declined before harvest in 1990, possibly due to drought conditions. The pattern of natality in 1991 closely mirrored the pattern of change in density, suggesting that reproduction, rather than immigration, was the predominant factor underlying the increase in density. Aerial activity, as measured by deposition traps and a rotary trap in the field, and a suction trap at the edge of the field, increased progressively during the growing season. Results from a short-term field eging technique, used to measure net migration rates, indicated that there was little immigration before July (thereafter high sampling variance, caused by aggregation in weedy patches, precluded meaningful analysis). □ *Araneae, Linyphiidae, spatial dynamics, winter wheat, density, natality, migration.*

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There are few studies of the population dynamics of predators. For example, Stiling (1988), in an examination of the incidence of density-dependence in invertebrate populations, quotes 62 population dynamics studies; of these 60 relate to phytophages, 2 to parasitoids and none to predators. There are also few population dynamics studies of migratory species, because of the methodological problems involved in quantifying migration. The present study, of the population dynamics of linyphiid spiders (the species concerned are all migratory predators), was undertaken to collect some basic data in this neglected area, and also because these species are known to be valuable predators of crop pests (Sunderland *et al.*, 1986). This paper summarises the main trends for total linyphiids; consideration will be given to individual linyphiid species in later publications.

### METHODS AND MATERIALS

Total spider density was measured throughout most of the growing season of 1990 in a 17ha field of winter wheat (c.v. Pastiche) in southeast England. In 1991, density, natality and migration were measured in a 3ha field of winter wheat (c.v. Riband), 24km from the 1990 study field. The fields were treated with agrochemical applications, following normal farm practice; insecticides were not required in either year.

### DENSITY SAMPLING

Twenty-five 144m<sup>2</sup> squares were marked out inside a 60 x 60m area (adjacent to one edge of the field in 1990 and 30m from the nearest edge in 1991). Fifteen density samples were taken at each sampling interval (approximately weekly) following a Latin Square design. The sample unit consisted of a randomly-selected 0.5m<sup>2</sup> area of ground delimited by a metal ring and sampled using a vacuum insect net (D-vac). Vegetation and the top 1cm of ground, within the 0.5m<sup>2</sup> sampled by D-vac, were then immediately hand-searched for spiders. The suction catch was kept at 10°C and returned to the laboratory for live-sorting. Therefore spiders were collected from 7.5m<sup>2</sup> of habitat (crop, ground surface and immediate sub-surface) on each occasion (Topping and Sunderland, 1992). The D-vac collected only about 50% of the total number of spiders present in a sample unit, the other 50% were uncovered by hand-searching (see also Sunderland *et al.*, 1987).

### NATALITY

Adult female linyphiids were collected from the field, adjacent to the 60 x 60m area, at weekly intervals and incarcerated individually in 9cm diameter plastic Petri dishes lined with moist filter paper. The dishes were returned immediately to a ventilated box in the study field and examined at weekly intervals. Mean daily temperatures in the Petri dishes did not diverge from field temperatures (measured on the ground

surface, under weed cover) by more than 1°C (warmer in spring, cooler in summer). The dishes were inspected at weekly intervals and the following statistics recorded (i) proportion of spiders producing eggsacs in the first week of incarceration, (ii) time (days) to emergence of spiderlings, (iii) number of spiderlings emerging, and (iv) number of undeveloped eggs (by dissection of the eggsac). These results were used, in conjunction with information on the density of adult females, to calculate daily natality rates for each species and then combined to give a composite spider natality curve.

#### NET MIGRATION RATE

Migration to and from small areas of the crop was suppressed by the use of ten stainless steel spider-proof cages. The cages were circular, 0.5m<sup>2</sup> by 1m tall, and made of mesh with 3 x 2.5 perforations mm<sup>-2</sup> (too small to allow passage of first instar linyphiid spiders). The bases of the cages were sealed with sufficient compacted soil to prevent entry or exit of any spiders. Total spider density inside the cages was assessed as above. Because the cages were moved to a new location within the Latin Square each week, there was assumed to be insufficient time for the processes of natality and mortality to be significantly affected by the changed microclimate inside the cages; therefore differences in the change in density from one week to the next between caged and uncaged parts of the crop were considered to be a measure of net migration.

#### AERIAL DENSITY OF SPIDERS

A 46cm Propeller Suction Trap (Taylor, 1955), with an air throughput of 70m<sup>3</sup> min<sup>-1</sup> and a sampling height of 142cm above the ground surface, located at the edge of the study field, was emptied daily. In addition, a rotary insect net was used to collect spiders within the field, 25cm above the top of the crop canopy. The 10m long rotor arm travelled at 6.3m sec<sup>-1</sup> and the 56 x 25cm net at the end of the rotor arm (which was designed to sample air isokinetically, (Taylor, 1962)) processed 53.8m<sup>3</sup> min<sup>-1</sup> and was also emptied daily. To measure rates of input of spiders into the field, a set of seven deposition traps were deployed at 15m intervals between the rotor and the 60 x 60m area. Each trap consisted of a 10cm deep, 1m<sup>2</sup>, fibreglass tray, filled with water and ethylene glycol (20:1) plus 1% detergent, fitting inside a 1.6m<sup>2</sup> metal tray containing the same fluid. The outer tray acted as a barrier to prevent spiders walking from the crop into the inner tray,

which therefore received only aerial immigrants. As the crop grew, the deposition traps were progressively raised on wooden supports to maintain the level of the fluid surface constantly at ca. 5cm above the top of the crop canopy. The traps were emptied at approximately weekly intervals.

Nomenclature follows Roberts (1987).

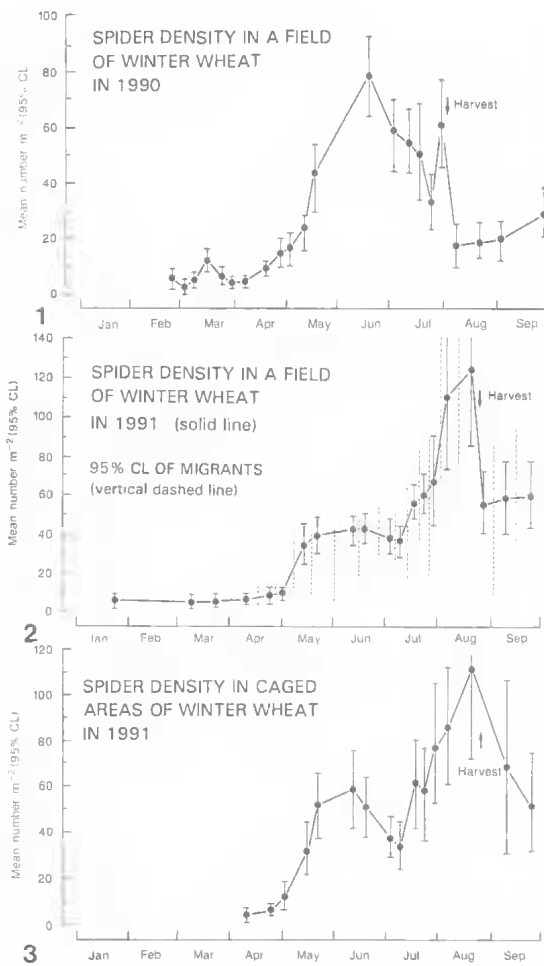
## RESULTS

The study was based on data from more than 39,000 individuals belonging to 53 species. 12 species were dominant (Table 1). All species belong to the family Linyphiidae, with the exception of the tetragnathid *Pachygnatha degeeri*. *Lepthyphantes tenuis* was the most abundant species in 1991 and the second most abundant in 1990. Species composition was similar in the two years, the only notable differences being that *Meioneta rurestris* was relatively more abundant in 1990, the reverse being true for *Oedothorax* spp. Here, all spiders are treated as a group.

In 1990, density of total spiders increased in spring to reach a peak of 78m<sup>-2</sup> on 18 June and thereafter declined, apart from a short-lasting peak (made up entirely of immature spiders) just before harvest (Fig. 1). The pattern was different in 1991 (Fig. 2); spider density built up in two steps (the first in May/June, the second in August) to reach a peak of 123m<sup>-2</sup> just before harvest. Mean air temperatures in June and July were slightly higher in 1990 (15.1°C) than 1991 (14.9°C), but rainfall was considerably lower (68mm in 1990 cf 191mm in 1991). The semi-drought conditions in the summer of 1990 may have had a deleterious effect on spider survival.

Species	1990	1991
<i>Meioneta rurestris</i> (C.L. Koch)	32.5	5.4
<i>Lepthyphantes tenuis</i> (Blackwall)	27.8	31.3
<i>Erigone atra</i> (Blackwall)	9.8	13.3
<i>Milleriana inerrans</i> (O.P.-Cambridge)	5.2	0.4
<i>Erigone promiscua</i> (O.P.-Cambridge)	5.0	6.3
<i>Erigone dentipalpis</i> (Wider)	4.2	5.0
<i>Pachygnatha degeeri</i> Sundevall	2.0	0.2
<i>Bathypantes gracilis</i> (Blackwall)	2.7	8.6
<i>Oedothorax fuscus</i> (Blackwall)	2.4	12.0
<i>Oedothorax retusus</i> (Westring)	2.1	3.9
<i>Panamomops sulcifrons</i> (Wider)	1.0	0.1
<i>Oedothorax apicatus</i> (Blackwall)	0.3	6.9
Others*	5.0	6.6

TABLE 1. Species composition of adult spiders in density samples in 1990 (n=1562) and 1991 (n=1457).



FIGS. 1-3. Total spider density in a field of winter wheat: 1990 (Fig. 1); 1991 (solid line) and 95% CL of number of migrants  $m^{-2}$  (vertical dashed lines) (Fig. 2); in caged areas, 1991 (Fig. 3).

Density in the caged areas of the crop in 1991 followed a similar pattern to that in uncaged areas (Fig. 3). 95% confidence limits increased during July and August (Figs 2, 3) due to aggregation of spiders in weedy patches of the crop (significantly more spiders in weedy than bare areas; paired t-test,  $n = 5$  dates,  $p = 0.05$ ).

The pattern of change in density with respect to time is examined, below, in relation to natality and migration for 1991.

Natality rates were  $c. 4m^{-2} day^{-1}$  in the spring, briefly  $10-15m^{-2} day^{-1}$  in late July, then  $8m^{-2} day^{-1}$  in August. The pattern of daily natality was similar to the patterns for immature spider density (Fig. 4) and total spider density (Fig. 2); this is

Date	M	95% CL
9 April	2.1	(-1.2- 5.4)
23 April	2.2	(-2.3- 6.7)
1 May	-2.0	(-8.7- 4.7)
14 May	2.7	(-11.8-17.2)
21 May	-12.8	(-29.5- 3.9)
11 June	-16.5	(-33.9- 0.9)
18 June	-8.0	(-23.1- 7.1)
3 July	0.7	(-13.2-14.6)
9 July	2.9	(-10.4-16.2)
17 July	-5.1	(-26.7-16.5)
23 July	1.8	(-20.5-24.1)
29 July	-9.5	(-43.8-24.8)
5 August	24.2	(-19.9-68.3)
19 August	12.7	(-41.4-66.8)
9 September	-10.0	(-52.7-32.7)
24 September	7.1	(-19.6-33.8)

TABLE 2. Indices of net aerial migration, M (95% CL), in 1991.

circumstantial evidence that reproduction (as opposed to immigration) is the predominant process driving increase in density of spiders in the field. Data on migration can be examined in the light of this hypothesis. Aerial activity of spiders, as measured by catches in the 1.4m suction trap at the edge of the field, tended to increase steadily from March to August, and this was followed by a much larger increase in September (Fig. 5). A similar pattern of aerial activity was evident inside the field, as indicated by the catch in deposition traps and in the rotary trap (Fig. 6). To assess whether there had been a net gain or loss of spiders from the field over a particular period, the density of spiders inside caged areas was compared with the density outside, to give an index of net migration (M);

$$M = (F2-F1)-(C2-F1) = F2-C2$$

where F1 and F2 are densities in the uncaged part of the field in weeks 1 and 2 respectively, and C2 is the density in the caged part of the field in week 2. (F2-F1 represents change in numbers due to natality, mortality and migration, whereas C2-F1 represents change in numbers due to natality and mortality alone, because migration was suppressed by caging). The standard error of M is calculated as the square root of  $[SE F2^2 + SE C2^2]$ ; the 95% CL's on M are therefore large because they are compounded of two standard errors. Values of M are shown in Table 2. Positive values indicate immigration and negative values indicate emigration. However, all 95% CL's span the range from negative to positive and therefore no significant net migration can be demonstrated.

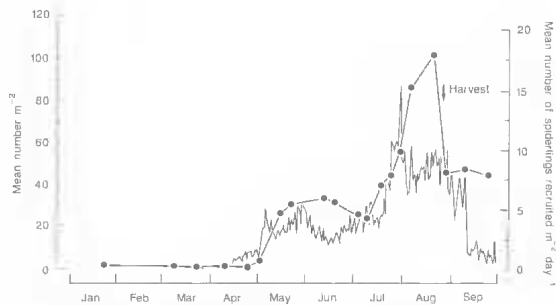
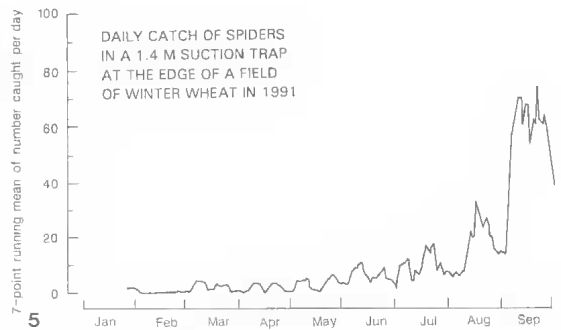


FIG. 4. Total immature spider density (●) and total spider natality (continuous line) in a field of winter wheat in 1991.

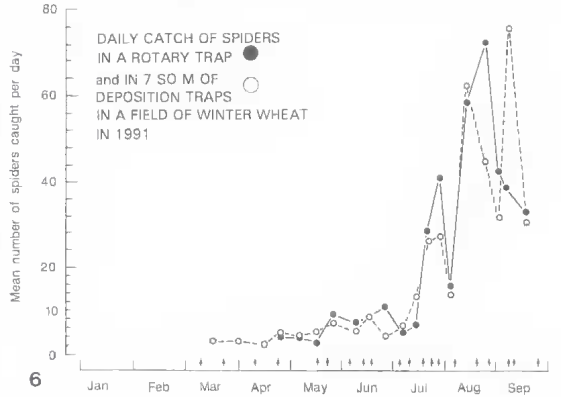
These 95% CL's are plotted on the curve of total spider density (Fig. 2); the extent of the dotted line above and below the density curve shows the amount of immigration and emigration, respectively, that could have occurred between any two dates. The following conclusions can be drawn; (i) any migration that may have occurred in April was small (i.e. on a similar scale to density sampling variance), (ii) if immigration occurred in May and June it must also have been on a small scale, but there could have been a large emigration, and (iii) in July, August and September 95% CL's were very large (due to spider aggregation, see above), with no obvious bias in favour of either immigration or emigration.

DISCUSSION

There appear to be no previous quantitative arachnological studies in which the seasonal patterns of natality and migration are compared with the seasonal pattern of density using consistent units. Examples of other arachnological studies involving density or natality estimation are given below. The majority of investigations where density has been measured are for grassland; peak



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FIGS. 5, 6. Daily catch of total spiders in winter wheat field in 1991. 5. In 1.4m suction trap at edge of field; 6. In rotary trap (●) and in 7m<sup>2</sup> of deposition traps.

densities of lycosid and linyphiid spiders vary greatly according to location (Table 3). Densities are often lower in graminaceous crops (Table 3). The peak spider density of 123m<sup>-2</sup> in the present study is comparable with, if somewhat greater than, densities recorded in cereals by other authors (Table 3). In common with the present investigation, nearly all the studies in Table 3 reported large confidence limits due to aggrega-

Species	Family	Habitat	Density	Author(s)
<i>Geolycosa godeffroyi</i> (L.Koch)	Lycosidae	pasture	1	Humphreys, 1976
<i>Trochosa terricola</i> Thorell	Lycosidae	grass heath	70	Workman, 1978
<i>Pardosa palustris</i> (Linnaeus)	Lycosidae	alpine meadow	9	Steigen, 1975
<i>Oedothorax fuscus</i> (Blackwall)	Linyphiidae	pasture	155	De Keer and Maelfait, 1987
<i>Erigone atra</i> (Blackwall)	Linyphiidae	pasture	318	De Keer and Maelfait, 1988
<i>Erigone arctica</i> (White)	Linyphiidae	dune grass	330	van Wingerden, 1977
Total spiders		<i>Festuca</i> grass	840	Duffey, 1962
Total spiders		rye grass	43	AlderwiereIdt, 1987
Total spiders		maize	49	AlderwiereIdt, 1987
<i>Oedothorax</i> and <i>Erigone</i>	Linyphiidae	winter wheat	53	Nyffeler and Benz, 1988
Total linyphiids		winter wheat	60	Fraser, 1982
Total spiders		winter wheat	75	Sunderland 1987

TABLE 3. Maximum density estimates (number m<sup>-2</sup>) in a range of arachnological studies.

tion of spiders. There seem to be no previous publications describing the seasonal pattern of spider natality, but a few authors (eg Steigen, 1975; Workman, 1978) have recorded natality at specific times of year. Schaefer (1978) estimated the egg density of the linyphiid *Floronina bucculenta* in grassland during the spring to be 98-151m<sup>-2</sup> depending on location. The maximum spring natality of the linyphiid *Erigone arctica* in coastal grassland was claimed to be 2584m<sup>-2</sup> (van Wingerden, 1977), which is considerably greater than the total natality (8 dominant linyphiids) of 789m<sup>-2</sup> between March and October in the present study; this difference may underly the relative sparseness of spiders in crops compared with natural grassland (Table 3). Although the intensity of aeronautic activity has been measured using sticky traps (Duffey, 1956, van Wingerden, 1977, Greenstone *et al.*, 1985), window traps (Meijer, 1976; De Keer and Maelfait, 1987, 1988) and suction traps (Dean and Sterling, 1985; Sunderland, 1987, 1991), there appear to be no previous attempts to directly quantify the impact of migration on population density. The use of short-term field cages in the present study provided useful estimates of the upper limits to migration (except when sampling variance became very large) and it is expected that this technique will yield better results when data are analysed for individual species. In addition, when the rotary trap has been calibrated, it should be possible to estimate rates of aerial immigration and emigration from a comparison of deposition and rotor catches.

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